

chambers were empty. If high ontogenetic and/or infraspecific variation is assumed, with the expansion rate ranging from 2.0 to 2.4, the respective values for the half whorl increment would lie between 1.8:1 and 2.8:1. Consequently, the assumption of Mutvei and Reyment that more than the last half whorl and probably parts of the inner whorls, are filled with liquid is incompatible with their experimental data. Their model is internally inconsistent. I believe that, for reasons of economy of shell construction, the actual liquid contained in ammonoid phragmocones rarely exceeded 10–15% of the total volume (i.e. the one to three last camerae).

Furthermore, most recently Dr. R. Cowen (oral communication at the Palaeontological Association's 'Phylogeny of Mollusca' colloquium in London, April 1974) has proposed that decoupling of the connecting rings of the siphuncle from the cameral liquid, *not* immersion in it, was required. Cowen suggests that this would prevent significant passive liquid exchange resulting from pressure differentials during the relatively rapid vertical movement powered by the hyponome; while the osmotic liquid exchange would be for buoyancy adjustment and more persistent (e.g. diurnal) vertical movements requiring only relatively slow exchange of liquid. Thus he regards the surface transport of liquid along the cameral walls towards the ventro-marginal siphuncle in uppermost position as a built-in braking system.

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#### REPLY TO WESTERMANN

MUTVEI: The osmotic regulation mechanism of the volumes of the cameral liquid in recent and fossil cephalopods has been reviewed by Denton (1974) who arrived at the conclusion that in ammonoids this mechanism cannot yet be interpreted in detail. This topic was only briefly touched on in our paper. The main stress was placed with the fact that in prosiphonate ammonoids, the formation of connecting rings has been delayed, which can only mean that several of the last-formed chambers must have been full of liquid. This condition is fundamentally different from that in all other fossil and recent shell-bearing cephalopods. According to Denton (1974), most recent squids are held neutrally buoyant by an ammonium compound in their tissues. It is significant here that the muscular tissue is greatly reduced and that these squids are not actively swimming animals. Their mode of life would appear to be similar to that of the ammonoids which had feebly developed retractor muscles and which for this and other reasons, discussed in our paper, do not seem to have been actively

swimming animals. Contrary to our interpretation, Westermann quotes an opinion that ammonoids were capable of 'relatively rapid vertical movements' by means of the hyponome.

REYMENT: Our results in fact support Westermann's adult migration hypothesis (cf. our paper, p. 635). The inaccurately worded and intuitive remark of mine, quoted in Westermann's first paragraph, needs qualification. This was not based on experiments and cannot be used for calculations. Even so, Westermann's note is well taken, although a better estimate for ceratites can be made by using results on variability (Reyment 1973, pp. 27-28). Computer simulation work I have done recently, using stochastic control theory in which the stochastic element was obtained from empirical information from a set of known variations, indicated for simulated ceratites a possible volume of cameral liquid of some 25-40% of the chambered volume for a range of shell types.

As regards the other comments made in Westermann's note, I beg to differ.

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